"One final paragraph of advice: do not burn yourselves out. Be as I am - a reluctant enthusiast....a part-time crusader, a half-hearted fanatic. Save the other half of yourselves and your lives for pleasure and adventure. It is not enough to fight for the land; it is even more important to enjoy it. While you can. While it's still here. So get out there and hunt and fish and mess around with your friends, ramble out yonder and explore the forests, encounter the grizz, climb the mountains, bag the peaks, run the rivers, breathe deep of that yet sweet and lucid air, sit quietly for a while and contemplate the precious stillness, the lovely, mysterious, and awesome space. Enjoy yourselves, keep your brain in your head and your head firmly attached to the body, the body active and alive, and I promise you this much; I promise you this one sweet victory over our enemies, over those desk-bound men and women with their hearts in a safe deposit box, and their eyes hypnotized by desk calculators. I promise you this; You will outlive the bastards."

Edward Abbey 1988

University of Alberta

DETERMINING BULL TROUT HABITAT AND PREY SELECTION (*Salvelinus confluentus*) USING SNORKEL SURVEYS AND STABLE ISOTOPE ANALYSIS

By

Ryan C. Popowich

A thesis submitted to the Faculty of Graduate Studies in partial fulfillment of the requirements for the Degree of Master of Science

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This thesis is dedicated to the memory of my grandfather, Adelard Malo

ABSTRACT

Bull trout populations are declining prompting considerable research aimed at describing habitat selection. However, observed patterns of habitat use are not static but depend upon intrinsic factors (*e.g.*, population dynamics, density dependence) in addition to commonly studied habitat variables (extrinsic factors). I used snorkel surveys and stable isotope analysis (S.I.A.) to assess density dependant habitat and diet selection in two fluvial bull trout populations. As predicted, bull trout (high and low density) consistently selected pool habitat however, at high densities, bull trout also selected habitat according to distributions of prey fish distributions. S.I.A showed bull trout to be highly piscivorous suggesting interspecific spatial relationships were driven by foraging. These relationships changed through time as focus shifted toward spawning. These findings support the idea that habitat selection can be an emergent property of biotic factors with individuals being driven by energetic cost (*e.g.*, competition) – benefit (*e.g.*, energy acquisition) trade-offs, an important consideration for future management strategies.

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DETERMINING BULL TROUT HABITAT AND PREY SELECTION (*Salvelinus confluentus*) USING SNORKEL SURVEYS AND STABLE ISOTOPE ANALYSIS

Introduction

In general, populations of bull trout (*Salvelinus confluentus*) are on the decline throughout their native range (Post and Johnston 2002, Wissmar and Craig 2004). Reasons include past mismanagement, migration barriers, competition and hybridization with invasive species, over-fishing, mis-identification, poaching, and habitat loss (Kitano *et al.* 1994, Rieman *et al.* 1997, Swanberg 1997, Dunham and Rieman 1999, Neraas and Spruell 2001). These disturbances, in combination with narrow habitat preferences, slow growth rates, late maturity, and in some instances, alternate-year spawning (Nelson and Paetz 1992, Post and Johnston 2002), have lead to decreasing population numbers, local extinctions, and numerous threatened designations throughout the native range in western North America (Rieman *et al.* 1997, Nelson *et al.* 2002). In response, considerable effort has been devoted to exploring relationships between bull trout occurrence and defined habitat variables.

A growing body of evidence suggests bull trout distributions are influenced by stream temperature, elevation, gradient, width, abundance of pools, and woody debris (Rieman *et al.* 1997, Watson and Hillman 1997, Dunham and Rieman 1999, Paul and Post 2001, Rich *et al.* 2003). However, important biotic factors that likely affect habitat selection, including presence or absence of other species, intra- and inter-specific competitive interactions, and predator-prey relationships, are rarely studied (Greenberg

1994, Watson and Hillman 1997, Dunham and Rieman 1999, Paul and Post 2001). For example, the role prey distributions play in driving adult bull trout habitat selection and distribution is not well understood, due in part to these studies being primarily conducted in small natural systems or in artificial streams (Greenberg 1994, Nakano *et al.* 1998, Spangler and Scarnecchia 2001, Rich *et al.* 2003). These interactions are likely significant in influencing bull trout distribution, and therefore deserve research attention.

Bull trout are top predators in eastern slope Rocky Mountain watersheds preying upon a variety of organisms ranging from stream macroinvertebrates to adult fish (Scott and Crossman 1973, Boag 1987, Nelson and Paetz 1992, Wilhelm *et al.* 1999). It follows that prey distributions and availability should play a contributing role in driving bull trout habitat selection behaviour. Furthermore, habitat selection can be an emergent property of population dynamics with individuals being driven by energetic cost (*e.g.*, predation, competition) – benefit (*e.g.*, energy acquisition) trade-offs, (Greenberg 1994, Nakano *et al.* 1998, Mushens 2003). Low densities of bull trout may afford individuals opportunity to occupy optimal foraging habitat that otherwise would be avoided due to high competition and / or predation potential. In these systems, prey are unlikely to be limiting and therefore bull trout spatial distributions should be driven by optimal habitat availability rather than prey distributions. Conversely, in areas of higher density some individuals would be forced to occupy sub-optimal habitats due to increased competition and risk of predation (Wissmar and Craig 2004). Higher densities of predators are more likely to be prey-limited and thus predator distributions should be more tightly correlated to that of their prey. Therefore, observed patterns of bull trout habitat use are not static but depend upon intrinsic (population dynamics and density dependence) as well as biotic

and abiotic habitat variables (extrinsic factors) (Greenberg 1994, Mushens 2003, Shepherd and Litvak 2004).

Spatial relationships between bull trout and potential prey are of limited informative value if it is not understood how or if predator and prey distributions affect prey consumption. Therefore a spatially explicit study of the community assemblage and bull trout trophic ecology was conducted on the Elbow and Sheep Rivers of the eastern slopes of the Rocky Mountains, Alberta. Snorkel surveys and stable isotope analysis (S.I.A.) were used to explore habitat selection and foraging behaviour of fluvial bull trout in relation to prey abundance and distribution.

Methods considered standard (*e.g.*, electro-shocking, angling, stomach content analysis) in examining fluvial predator-prey interactions do not provide adequate data resolution to properly address the questions posed here. Recent advancements in survey techniques (snorkel surveys) and trophic analysis using stable isotopes provide opportunities to gather fine-scale data in large geographic systems. S.I.A. is recognized as a powerful analytical tool to analyze dietary history, re-construct aquatic food webs, and describe trophic interactions in a non-invasive manner (Vander Zanden *et al.* 1999, Harvey and Kitchell 2000, Grey 2001). Because S.I.A. provides a more complete and temporally integrated description of diet history it is superior to conventional stomach content analysis (Grey 2001). Similarly, snorkel surveys provide the opportunity for non-invasive sampling, especially beneficial when studying threatened species. Given adequate water clarity, snorkel surveys are faster, more reliable, logistically easier, significantly cheaper, and are non-invasive relative to electrofishing, netting, seining, or angling, when collecting abundance and distribution data. Further, snorkeling also

provides the opportunity to study populations residing in larger fluvial systems rarely addressed in the literature.

The importance of prey distribution in influencing bull trout habitat selection and dietary composition in large, fluvial systems remains largely undescribed, especially with respect to population density. The Elbow and Sheep rivers are similar in most habitat variables, however resident bull trout populations differ in that the Sheep River has higher bull trout densities and a higher bull trout : prey ratio. These differences were exploited to assess the role of density in bull trout habitat and prey selection and ultimately, to evaluate the importance of these phenomenon in declining bull trout populations in the eastern slopes of the Rocky Mountains. The objective of this work was to test the hypothesis that habitat selection in dense bull trout populations (*i.e.*, characterized by high predator: prey ratios) can be predicted by prey distributions, and in contrast, habitat selection will be driven by habitat type (pool vs. riffle) in low density bull trout populations. Bull trout – prey associations should diminish through time as water temperatures decrease and bull trout shift focus from active foraging to spawning behaviour. Related secondary objectives include i) reconstruction of the aquatic food web of the Elbow River (only), ii) an analysis of size- and tissue-dependant isotope variation and most importantly, iii) combining stable isotope dietary data with habitat selection findings to explore bull trout foraging strategies. If different size classes of bull trout differentially depend on alternative prey species, the management of those prey species becomes a significant component of successful bull trout conservation and management.

Materials and methods

Study area

This study was conducted on the Elbow (sampling area elev. 1420m) and Sheep Rivers (sampling area elev. 1260m) both located along the eastern slopes of the Rocky Mountains, Alberta (Fig. 1). The Elbow River watershed (1230 km^2) is approximately twice the size of the Sheep (595 km^2), resulting in approximately 1.5 times the average annual discharge (Elbow: 8.35 m^3/s, Sheep: 5.21 m^3/s). The rivers are comparable in terms of geomorphology, temperature regime, and fish assemblage including native bull trout, cutthroat trout (*Oncorhynchus clarki lewisi*), mountain whitefish (*Prosopium williamsoni*), and members of the Cyprinidae, Catostomidae, and Cottidae families. Non-native species in both include brook trout (*Salvelinus fontinalis*), brown trout (*Salmo trutta*), and rainbow trout (*Oncorhynchus mykiss*) (Henderson and Peter 1969, Nelson and Paetz 1992).

Microhabitat selection

Snorkel surveys were used to quantify fish distributions on 6 kms of river downstream of an impassable waterfall on each river during July – October 2003 and 2004 (Fig. 1). These sections encompass the majority of known bull trout spawning habitat in each river (Jim Stelfox, Area Fisheries Biologist, pers. comm., Popowich unpublished data 2003). The 6 km survey sections were divided into 60, 100 m sampling units. This scale was chosen based on previous experiments and a pilot project using 1 km sampling units that did not provide accurate representation of fish assemblage dynamics known to occur at much smaller scales (Watson and Hillman 1997, Popowich,

unpublished data 2003). Bull trout densities (fish / m^2) were calculated in these sections using fish counts and river dimensions measured at average flow.

Snorkel surveys were conducted by two snorkelers proceeding downstream simultaneously. The narrow rivers easily allowed observation of the entire width by two snorkelers. Snorkelers counted and estimated the lengths of separate species to avoid repeated counts of the same fish. Members of the Cyprinidae, Catostomidae, and Cottidae families were not encountered or enumerated. All observed fish were identified, counted, estimated for fork length (FL) (cm) and grouped by size (0-9 cm, 10-19 cm, etc.). Surveys commenced when spring flows and turbidity allowed adequate visibility for snorkelers (July, both years). Surveys were conducted between 10:00 and 17:00 hrs. approximately weekly until bull trout vacated the survey section after spawning (October) (Table 1). Spatial relationships between species during snorkel surveys were established using Pearson's correlation coefficients. To address type I error, Bonferroni-corrected α values were used (Wasserman 2004).

Stream habitat composition was visually estimated for each 100 m study reach on each replicate survey swim, and defined as run / riffle or pool. Run / riffle habitat was defined as any flowing portions of the river that moved rapidly in comparison to slow moving or stagnant portions of the river, and included flows ranging from small riffles to waterfalls (>1 m). Pool habitat was defined as still water or water that showed a noticeable reduction in velocity as compared to the closest reference run regardless of depth. Preliminary snorkeling observations did not reveal any discernable differences in fish activity to warrant further categorization of stream flow.

Estimation error

Habitat classification error was established using digital photographs taken from light aircraft approximately 120 m above the river. Grids were superimposed on aerial photographs of four, 100 m sections and each quadrant was visually scored as either run / riffle or pool. Estimate error was determined by comparing average run / riffle vs. pool proportions (estimated by snorkelers) to proportions calculated from digital photographs.

To establish error in fish count data, a 100-m snorkel section was randomly selected from within each 1 km study section (n = 6) of the Elbow River. First, a single, snorkeler chosen at random swam the 100-m section and counted all observed fish. After returning to the head of the reach, the survey was repeated with the addition of another snorkeler. One snorkeler was added on each successive pass until a total of five snorkelers were swimming the survey section simultaneously. Given the average width of the river (mean +/- SD = 22.4 +/- 6.29 m) in the 6 km study section, it would be inefficient to snorkel the survey sections with more than five snorkelers. All were experienced at surveying rivers. Mean values for each snorkeler grouping (1 through 5) were calculated using counts from each of the six survey sections. Although small numbers of fish were likely missed (*e.g.*, juveniles in peripheral substrate), additional snorkelers would not have detected them. Because electrofishing could not be used to sample these sections, the mean counts from the five divers are considered the best possible site-specific diagnostic measure of this technique.

To establish fish length estimation error, snorkelers estimated fish lengths while anglers caught (hook and line) and measured (FL (mm)) the snorkeler-observed fish.

This method was also used to calibrate and standardize fish-length estimating skills before snorkeling surveys commenced.

To address issues of pseudoreplication associated with repeated snorkel surveys on the same sections of river, correlation coefficients for bull trout – prey fish, and pool – run / riffle were calculated for each survey for 14 (8 Elbow, 6 Sheep) randomly chosen 100 m sections. Temperature and discharge profiles for each river were also collected to provide support for temporal independence of the survey sections throughout the duration of the snorkel surveys.

Stable isotope analysis

All samples were collected during July - October 2003 and 2004 throughout the 6 km snorkel survey reach on the Elbow River (Fig. 1). Fish samples were collected using hook and line, electrofishing, and minnow traps. All fish were measured (FL (mm)) and weighed (g). Fish tissues sampled included, anal and adipose fins, whole blood, stomach contents and some whole individuals. Fin clips were wrapped in tin foil, placed in scale envelopes, and air dried at room temperature (min. 24 hrs) before being frozen at -20°C. Stomach contents were collected using gastric lavage (Light *et al.* 1983) while whole blood was collected from the caudal vein by syringe and frozen at -20°C within 6 hrs of collection. Sodium citrate ($C_6H_8O_7Na_3$) solutions were used in the syringes to prevent blood clots. Sodium citrate was chosen over heparin because heparin is a derivative of porcine intestinal mucosa and so could significantly alter the ^{15}N signature of the blood. Prior to sampling, fish were anesthetized using clove oil [~1mL / L river water] (Jim Stelfox, Area Fisheries Biologist, pers. comm.). Condition factors for sampled bull trout

were calculated using Fulton's body condition (K) where $K = 0.25 (W / TL^3) * 100$, where W is live weight (g) and TL is total length (cm) (Craig *et al.* 2005).

Macroinvertebrates (Orders Diptera, Ephemeroptera, and Plecoptera) were used to establish isotopic baseline signatures. Samples were collected from throughout the watershed using Serber samplers, drift samplers (minimum 24 hr sets), and kick-nets between July 23 – 29, 2003 and 2004. All macroinvertebrate samples were identified to Order (Clifford 1991) and kept live for 6-24 hrs to allow for evacuation of gut contents before being preserved in ~70% ethanol (ETOH). The effects of short-term (6 mo) ETOH preservation on $\delta^{13}C$ and $\delta^{15}N$ ratios in animal tissue are variable (Bosley and Wainright 1999, Sarakinos *et al.* 2002). Because some samples in this study were preserved for longer periods (18 mo.), a small pilot study was carried out comparing the long-term preservation effects of ETOH, as well as addressing other limitations of stable isotope analysis including temporal, spatial, and individual isotopic signature variation within the Elbow River watershed. This also allowed for a comparison of baseline isotopic signatures from areas outside of the primary sampling area.

Samples were analyzed for isotopic ratios of nitrogen ($^{15}N/^{14}N$) to establish trophic position and carbon ($^{13}C/^{12}C$) to trace primary productivity (Peterson and Fry 1987). $\delta^{13}C$ values are used to trace primary production as there is minimal fractionation (~1‰) between trophic levels (DeNiro and Epstein 1978). However, $\delta^{15}N$ becomes enriched (3-5 ‰) at each trophic level enabling it to be used to establish trophic position (Minagawa and Wada 1984, Peterson and Fry 1987, Hobson and Clark 1992). Samples were analyzed using a Thermo-Finnigan Delta^{plus} Advantage gas isotope-ratio mass spectrometer interfaced with a Costech Analytical ECS4010 elemental analyzer at the

Colorado Plateau Stable Isotope Laboratory, University of Northern Arizona, using standard techniques. Isotope ratios are expressed in delta (δ) notation as parts per thousand (‰) relative to a standard using the equation: $\delta^{15}N$ (‰) = [(R_{sample} / $R_{standard}$) – 1] x 1000, where R = molar ratio of ^{15}N / ^{14}N for nitrogen (^{13}C / ^{12}C for carbon). Reference standard for N was atmospheric nitrogen and Pee Dee belemnite limestone for C. On average, analytical precision of standards was better than 0.1 ‰ for carbon and 0.2 ‰ for nitrogen. Ten percent of the samples were run in duplicate to establish analysis consistency.

All tissue samples were dried at 50-60°C for 24-72 hrs. Samples were then homogenized using scissors and a mortar and pestle, weighed (1+/- 0.02 mg), and sealed in 5 X 9 mm tin cups following standard stable isotope sample preparation techniques. Lipid removal and / or acid washing of samples can alter isotopic ratios, inflate variance, and reduce statistical power (Bosley and Wainright 1999, Lancaster and Waldron 2001, Sotiropoulos *et al.* 2004) and therefore were not performed here.

Baseline isotopic signatures from stream macroinvertebrates collected in 2003 and 2004 did not differ significantly (Popowich and Williamson, unpublished. data 2005), so combined species-specific mean values from both sampling years were used to reconstruct the Elbow River food web (Vander Zanden *et al.* 2003).

All statistical analyses were performed using SPSS 11.5 (Chicago, IL). The level of statistical significance was set at $p < 0.05$ for all tests. Data were checked for normality and equality of variance (where appropriate) before being used in parametric tests.

Results

Population comparisons

Bull trout densities in the Elbow and Sheep rivers were significantly different (independant samples *t*-test (2-tailed), $n = 12$, $p = 0.043$). On average the Sheep River supported 7.2×10^{-4} bull trout (all sizes) / m^2 (SD +/- 4.5×10^{-4}), approximately three times the density of the Elbow River population (2.5×10^{-4} fish / m^2 +/- 1.7×10^{-4}). The difference between the two systems was particularly pronounced with regards to adults ('adult', 'mature', or 'predatory' refer to bull trout greater than 300 mm FL).

* (>300 mm) (independant samples *t*-test (2-tailed), $n = 12$, $p = 0.026$) with Sheep River adult bull trout densities (7.0×10^{-4} fish / m^2, +/- 4.5×10^{-4}) existing at approximately five times the density of their Elbow River counterparts (1.33×10^{-4} fish / m^2, +/- 9.53×10^{-5}). Also, the average ratio of adult bull trout to prey fish densities was ~8.5x higher in the Sheep than in the Elbow River.

Microhabitat selection

Pearson correlation coefficients indicated that spatial associations between predatory bull trout and other species (potential prey) vary through time (Table 2, Fig 2). No significant spatial relationships were found in the Elbow River, however significant spatial relationships were present in the Sheep River during July, August, and into September 2004. Additional comparisons using different size categories of prey species (*e.g.*, 0 - 400 mm, 0 - 300 mm, etc.) yielded similar results.

With respect to habitat selection, both Elbow and Sheep River adult bull trout showed strong selection for pool over run / riffle habitat. Pool favoritism was temporarily interrupted during spawning on the Sheep River when adults showed strong

selection for run / riffle habitat during spawning (Table 3). Juvenile bull trout (<300 mm) habitat use did not differ from expected distributions based on available pool and run / riffle habitat. The only exceptions were two dates (July 22, Aug. 5) on the Elbow River.

Estimation error

There was no significant difference between pool vs. run / riffle habitat estimates made by snorkelers and those calculated using aerial photos (paired *t*-test, $n = 4$, $p = 0.361$). Although not statistically significant, snorkelers generally over-estimated run / riffle habitat and under-estimated pool habitat (mean +/- SD = 16.5% +/- 5). Significant differences were found between mean counts (average of all fish seen by 1, through 5 snorkelers calculated across the six test survey sections) of fish (Table 4) (repeated measures ANOVA, $p = 0.035$). Variation was relatively constant ranging from SD 3.2 (1 snorkeler) to SD 4.7 (3 snorkelers). Species-specific count differences were found for whitefish (repeated measures ANOVA, $p = 0.02$) and brook trout ($p = 0.02$).

With respect to size estimation, snorkelers categorized 33 of 38 (86%) of the test fish into the correct category over the course of the study. The average error of length estimation of the five incorrectly identified fish was 3.8 cm (SD 0.25 cm).

To address pseudoreplication issues associated with fish counts and habitat estimates on repeated surveys, correlation coefficients were calculated between bull trout and prey (all species, all sizes) counts at 14 randomly selected sites on both the Elbow and Sheep Rivers. Correlation values varied through time demonstrating sample site independence through time (Table 5). Further, river discharge (Figs 3 and 4) and temperature data (Fig. 5) were collected to further document temporal variability in the study sites throughout the survey period. Correlation coefficients were also calculated

between pool and run / riffle estimates. The values were high (~ 1) for each random site on both the Elbow and Sheep rivers suggesting that habitat was constant throughout the research period despite changes in river discharges.

Stable isotope analysis

Both sampling years were used to reconstruct the Elbow River foodweb. 2003 sampling focused on adult (>300 mm) fish, while 2004 sampling focused on juveniles. Comparing bull trout inter-year isotopic signature variability is complicated by a positive relationship between length and $\delta^{15}N$ for several species. Therefore, stream macroinvertebrate signatures were assessed to support the combined use of samples collected over the two years. If inter-year isotopic variation differences existed, the effects would be seen most easily in aquatic macroinvertebrates because of greater turnover rates of isotope ratios in small organisms.

Correlation coefficients were calculated to quantify $\delta^{13}C$ and $\delta^{15}N$ variation between randomly chosen duplicate tissue samples (analyzed to establish S.I.A. reliability). Mass spectrophotometer analyses were highly consistent (Pearson correlation, $n = 31$, $\delta^{15}N$: $r = 0.991$, $\delta^{13}C$: $r = 994$, $p < 0.0001$ for both) (Figs. 6 and 7). Additionally, correlation coefficients were calculated to quantify $\delta^{13}C$ and $\delta^{15}N$ variation between individual species (Table 6). All correlations were significant at the $\alpha = 0.05$ level with the exception of $\delta^{15}N$ ratios of rainbow and cutthroat trout. Repeated samples for each of these species were highly correlated ($r > 0.95$), however sample sizes ($n = 3$ for both species) were too low for the correlations to be statistically significant.

Anal and adipose fin signatures were compared to address tissue dependant turnover rates. Significant differences between the $\delta^{15}N$ values of adipose and anal fins

(Δ mean 0.28 +/- 0.23 ‰ SD; paired samples *t*-test, $n = 83, p < 0.0001$) (Table 7) were found when all samples from all species were analyzed together (Fig. 8). With respect to individual species, significant differences were found between the $\delta^{15}N$ values of bull trout ($n = 39, p = 0.010$), and brook trout ($n = 6, p = 0.002$) anal and adipose fins. There were no significant differences found between the $\delta^{15}N$ values of cutthroat trout ($n = 16$, $p = 0.116$) or mountain whitefish ($n = 20, p = 0.070$) (Table 8).

Further, there were no significant differences between the $\delta^{13}C$ values of anal fins compared to adipose fins ($n = 83, p = 0.123$) when all samples from all species were analyzed together (Fig. 9). The average difference in anal and adipose $\delta^{15}N$ signatures was 0.74 (+/- 0.50 ‰ SD) (Table 7). There were significant differences found between the $\delta^{13}C$ values of bull trout ($n = 39, p < 0.001$), mountain whitefish ($n = 20, p < 0.001$), and cutthroat trout ($n = 16, p = 0.008$) (Table 8). However, there were no significant differences between the $\delta^{13}C$ values of anal fins compared to adipose fins ($n = 6, p = 0.196$) for brook trout. Bull trout blood samples and anal fin signatures were also compared; no significant differences were found for $\delta^{13}C$ ($n = 5, p = 0.075$) or $\delta^{15}N$ ($n = 5, p = 0.527$).

To assess broader inter-tissue variability, adipose, anal, caudal, dorsal, pelvic, and pectoral fins, and white muscle from brook trout were assayed. No significant differences between $\delta^{15}N$ (1-way ANOVA, $F_{6,27} = 0.239, p = 0.960$), or $\delta^{13}C$ ($F_{6,27} = 0.146, p = 0.988$) (Figs. 10 and 11) signatures of any of the tissue types.

Foodweb reconstruction

As no significant differences between tissue-specific signatures were found (*see discussion for further explanation*), the Elbow River food web was reconstructed using

anal fins due to a large available sample size (n = 175). $\delta^{15}N$ and $\delta^{13}C$ values for fish and macroinvertebrate species are displayed as individuals (Fig. 12) as well as means +/- SD (Fig. 13). Foodwebs are typically displayed as mean (+/- SD) values as in Figure 13 because groupings are more distinct and trophic levels more clearly defined; however isotopic variability may be masked (illustrated by the differences between Figs. 12 and 13). Because this variation is important, results and discussion will be based on both plots, in addition to Figure 13 that illustrates size-dependant bull trout signatures.

Stable isotope analyses clearly show that adult bull trout diets are comprised almost exclusively of fish (Figs. 12 and 13). Brook trout, cutthroat trout, mountain whitefish, and rainbow trout comprise the majority of the diet (at similar proportions), and juvenile bull trout were used to a lesser extent. There is no indication of macroinvertebrate utilization in the diet of adult bull trout. Interestingly, some mountain whitefish and juvenile bull trout (Fig. 12) had $\delta^{15}N$ values higher than those of some predatory bull trout, indicating that they are feeding at a comparable trophic level.

All bull trout stomachs sampled for contents were empty. Condition factors for bull trout with empty stomachs (mean +/- SD = 0.99 +/- 0.16 SD) were consistent with the conditions factors of all bull trout sampled throughout the study (0.99 +/- 0.16 SD) as well as those (K = 1 – 1.19) calculated by Tripp *et al.* (1979) from bull trout in the Elbow River.

With respect to size dependant changes in isotopic signatures, $\delta^{15}N$ values of prey fish (mountain whitefish, brook, cutthroat, and rainbow trout), are less size-dependant when compared to bull trout (R^2 = 0.79) (Fig. 15). Regression analyses show that

rainbow trout ($R^2 = 0.62$) and cutthroat trout ($R^2 = 0.40$) show stronger length - $\delta^{15}N$ relationships than do brook trout ($R^2 = 0.17$) and mountain whitefish ($R^2 = 0.01$).

With respect to the middle trophic grouping, juvenile bull trout, cutthroat trout, mountain whitefish, and rainbow trout occupy very similar feeding niches (Fig. 16). When exotic brook trout and rainbow trout and native bull trout, cutthroat trout, and mountain whitefish are plotted in a foodweb diagram based on S.I.A. there is significant overlap indicating a shared diet (Fig. 17).

Discussion

Microhabitat selection

The hypothesis that spatial distributions of high density populations of bull trout (Sheep River) are related to prey distributions was supported. Additional comparisons using different size categories of prey (*e.g.*, 0 - 300, 0 - 400 mm etc.) yielded similar results, suggesting that prey presence, rather than prey size, is the important factor in the relationship. The relationship between predatory bull trout and prey distributions was significant throughout the summer sampling period. This was expected because increased water temperature in summer and subsequently, metabolic rates and positive growth of bull trout, result in increased foraging activity (Mushens 2003). These findings suggest the distribution of prey species is an important factor driving habitat selection in high density populations of bull trout. This is significant given that distributions of prey fish are rarely incorporated into habitat selection models of bull trout and are rarely mentioned as important bull trout habitat features.

As predicted, the strength of these associations diminished through time as water temperatures decreased and spawning activity increased. Figure 2 clearly demonstrates

this trend with the Elbow River showing a similar pattern. Although none of the predator prey relationships on the Elbow River were significant, the similarity between the trends observed on both rivers offers additional support to the density-dependant habitat selection hypothesis. At lower densities, the trend is present, but weaker. Additionally, the patterns show similar fluctuations through time suggesting that bull trout populations in comparable systems experience similar shifts in habitat selection behaviour during transitions between biologically significant periods (*e.g.*, summer foraging - spawning).

The hypothesis that bull trout spatial distributions in lower density bull trout populations would be driven by habitat type rather than prey fish distributions was supported. However, predatory bull trout exhibited strong selection for pool habitat on both the Elbow (low-density) and Sheep (high-density) Rivers. As predicted, large predatory fish dominated deeper, slow moving water in both rivers where energetic demands and mammalian and avian predation are minimized, consistent with other studies (Bonneau and Scarnecchia 1998, Wissmar and Craig 2004).

The only exception to bull trout selection for pool habitat occurred during the spawning period when run / riffle habitats were favoured. Bull trout spawning and egg incubation requirements coincide with shallow, flowing water usually associated with ground-water inputs (Baxter and McPhail 1999, Baxter and Hauer 2000). It should be noted that this was observed only in the Sheep River and not the Elbow River. This is likely due to unseasonably high water levels on the Elbow River during spawning. River conditions prevented observation from occurring during periods when bull trout counts on spawning grounds are typically highest (Popowich unpublished data 2003).

Juvenile bull trout were distributed according to habitat availability. These findings are consistent with published work suggesting that small bull trout typically avoid deeper water and use shallow stream margins (Spangler and Scarnecchia 2001). Juvenile bull trout exhibited a slight shift from favoring pool habitat when adult densities were lowest, to expected distributions (based on availability) as adult presence increased. Juveniles were expected to exhibit strong run / riffle selection due to increased competition and risk of predation from adult bull trout. This was supported somewhat in that juveniles did occupy proportionally more run / riffle habitat however, not significantly more than expected based on habitat availability. At higher densities proportional use of run / riffle habitat would likely increase.

In summary, it was demonstrated that pool habitat and the presence of prey species are significant components of bull trout habitat selection, especially in higher density bull trout populations. However, additional study is required to more fully understand the role that density and predator-prey interactions play in bull trout habitat selection. For example, although densities of bull trout in the Sheep River (7.2×10^{-4} bull trout / m^2) were approximately three times higher than in the Elbow River (2.5×10^{-4} / m^2), bull trout densities in the Sheep River were 83 times lower than in parts of the North Saskatchewan River (6.0×10^{-2} / m^2) and 42 times lower than in portions of the Athabasca River (3.0×10^{-2} / m^2) (Michael Sullivan, Provincial Fisheries Science Specialist, pers. comm.). Based on data from these systems, inclusion of additional systems representative of the full range of naturally occurring bull trout densities, especially those near carrying capacity, would be a valuable test of this hypothesis. Whether these systems remain in Alberta is unknown.

In addition, the habitat selection hypotheses were structured from a predatory perspective which ignores half of the predator-prey relationship. It may seem intuitive that large bull trout should select habitat near potential prey however, predators can elicit avoidance behaviour in prey and alter habitat selection (Greenberg 1994, Spangler and Scarnecchia 2001). Further, the spatial scale at which this density-dependant relationship becomes established is undoubtedly influenced by available habitat. In other words, as density increases and high-quality habitat becomes limited, it is possible that bull trout – prey associations become stronger because available habitat becomes limited and the spatial buffer between predator and prey decreases. To fully understand the dynamic spatial relationship resulting from these interactions, both predatory and prey behaviour must be independently assessed at a biologically relevant scale. To establish this in a more comprehensive manner in a study such as this, habitat availability in the study sections needs to be quantified, and habitat selection trends need to be established for prey species.

Estimation error

Snorkel surveys were shown to be highly effective. Diagnostic experiments on snorkeler estimation of habitat, count, and length all showed that two snorkelers can effectively survey fish populations in fluvial systems of this size, where other techniques are limited by practicality and safety. Electrofishing and angling were attempted in these systems and found to be unsafe and impracticable in comparison. Snorkel observations can be limited by bias toward larger fish, and salmonid diel activity, especially amongst juveniles (Jackober *et al.* 2000, Baxter and McPhail 1997, Gries at al. 1997), thus juvenile fish were likely underestimated by snorkelers in this study. Small fish (<200

mm) were captured during electrofishing surveys in the snorkel section (Popowich unpublished. data). Typically such individuals would not been seen by snorkelers given the fish's position on or in the substrate. While this is a limitation of the snorkeling technique, it is unlikely that the distribution of these fish influenced habitat selection by larger bull trout occupying deeper, mainstream pools. With respect to variation in salmonid diel activity, night snorkel surveys could not be safely conducted in this study and therefore any differences in diel activity are irrelevant to this work.

Stable isotope analysis

Repeated analyses of samples for $\delta^{15}N$ and $\delta^{13}C$ were found to be highly consistent (Δ <0.5 ‰ among duplicate samples), suggesting that isotope preparation techniques, laboratory analyses, and subsequent results are reliable (Figs. 6 and 7). With respect to tissue-dependant variation, statistically significant differences were found between adipose and anal fin signatures; however, the statistical tests used are likely too powerful and differences are not likely biologically meaningful. Duplicates within 0.5 ‰ are considered to be consistent (Dr. Richard Doucett, Colorado Plateau Stable Isotope Laboratory, pers. comm.). Taking this into consideration, significant biological differences were found between anal and adipose $\delta^{13}C$ signatures in all species (grouped), bull trout, and mountain whitefish and $\delta^{15}N$ signatures in brook trout. Although these results are inconsistent among species and between isotopes, additional tissue, and species- and isotope-specific research could reveal important and useful trends.

With respect to bull trout, it was expected that turnover rate would be highest in blood, followed by anal and adipose fins respectively because physical abrasion with substrate might result in higher turnover rate in anal fins compared to adipose fins. Since

differences between tissue types were biologically inconsistent, the most parsimonious explanation of these data is that bull trout diet is invariant over the time periods assayed via S.I.A.here. If bull trout diets remained consistent over time periods longer than that of tissue turnover rates, all sampled tissue types would reflect this diet regardless of turnover rate. Sodium citrate ($C_6H_8O_7Na_3$) may have altered the blood carbon ratios, however, this is unlikely given the small amount of solution (100μL) used. Similarly, no statistically significant differences were found between $\delta^{15}N$ or $\delta^{13}C$ values from brook trout adipose, anal, caudal, dorsal, pelvic, pectoral or white muscle tissue. Like bull trout, perhaps diets are invariant over the time periods assayed via S.I.A. Further, tissue turnover rates and fractionation in these tissues may be temporally comparable or perhaps differences are undetectable by current S.I.A. methods. Larger sample sizes of all sizes classes would be beneficial.

There are clear inconsistencies between individual species and tissue types studied here. These results lend support as to why species-specific and tissue-specific differences must be taken into consideration in stable isotope studies. Tissue-dependant isotopic signature variability is a growing issue in stable isotope literature. Gannes *et al.* (1997) stressed the importance of more fully understanding the sources of isotopic variation before conclusions about ecological interactions can be formulated however, published results in this area are inconsistent. Isotopic fractionation values vary reflecting different species, growth rates, body size, age, condition (starvation), diets, tissue types, and life history strategies (Minagawa and Wada 1984, Peterson and Fry 1987, Hobson and Clark 1992 McCarthy and Waldron 2000). With respect to isotopic variation in fish for example, Dempson and Power (2004) found Atlantic salmon adipose

$\delta^{13}C$ signatures to be 0.52‰ more enriched than muscle and adipose $\delta^{15}N$ signatures to be 0.49‰ more depleted relative to muscle. In contrast, McCarthy and Waldron (2000) found no statistical differences between $\delta^{13}C$ and $\delta^{15}N$ values between white muscle and adipose tissue in brown trout. Inconsistency in published data further illustrates that species dependant results must be taken into consideration when reconstructing a multi-species food web. Tissue turnover is one of many sources of variation associated with S.I.A. however it may prove to be a valuable tool describing temporally dependant food habits. Although this study did not fully address these issues, the results of this work show that additional research is required to more efficiently use tissue dependant isotope data.

Foodweb reconstruction

S.I.A. clearly defined three distinct trophic levels of consumers within the Elbow River watershed; i) primary consumers represented by stream macroinvertebrates, ii) secondary consumers comprised of brook trout, juvenile bull trout, cutthroat trout, rainbow trout, and mountain whitefish, and finally iii) adult bull trout as tertiary consumers. With respect to the second trophic level, S.I.A. also illustrated that introduced brook and rainbow trout occupy feeding niches that directly overlap those of native cutthroat trout, mountain whitefish, and juvenile bull trout (Figs. 16 and 17). This direct dietary overlap may be contributing to the observed continued decline of bull trout in the Elbow River (Nakano *et al.* 1998).

Bull trout become increasingly more piscivorous with size. Adult bull trout (>300 mm) are highly piscivorous, preying upon brook trout, juvenile bull trout, cutthroat trout, rainbow trout, and mountain whitefish whereas juvenile bull trout (<300 mm) are

primarily insectivorous. Figures 12 and 13 illustrate the importance of analyzing size categories separately, especially among cannibalistic top predators. Prey preferences observed here are consistent with published findings (Tripp *et al.* 1979, Boag 1987, Wilhelm 1999, and Beauchamp and Van Tassel 2001). Further, these data provide support for the *a priori* prediction that insectivorous juvenile bull trout shift to become piscivorous as gape-limitation is overcome with growth (Figures 13 and 14). However, data resolution is not adequate to detect the specific period of prey shift; this would require an extensive increase in sampling effort focused on bull trout between 200 and 400 mm. Graphical displays of the data collected during this study do not provide adequate resolution to isolate a distinct shift. Brown trout are known to exhibit a similar shift in prey at the 300-400 mm size, although interestingly the transition is not reflected in isotopic signatures (Grey 2001). Trout typically experience an omnivorous stage in transition from insectivory to piscivory (Grey 2001). A similar phenomenon would help explain the lack of a distinct prey shift in Elbow River bull trout.

No stomach contents were recovered from any of the bull trout sampled in this study. This contrasts with Tripp *et al.* (1979), Boag (1987) and Beauchamp and Van Tassel (2001), where only 12%, 34% and 6%, respectively, of bull trout sampled had empty stomachs. However these data reflect much larger sample sizes and include greater sampling effort of smaller fish. Stomach samples from smaller, insectivorous fish are more likely to contain prey remnants given that small fish have higher metabolic demands, greater access to prey, and lower energetic values associated with stream macroinvertebrates. Lack of stomach contents could indicate that bull trout in the Elbow River were prey limited. However, condition factors for bull trout without stomach

contents (mean +/- SD = 0.99 +/- 0.16, n = 4) in addition to all bull trout sampled throughout the study (0.94 +/- 0.17 SD, n = 94) were consistent with the condition factors calculated by Tripp *et al.* (1979) using bull trout from the Elbow River. This suggests that Elbow River bull trout are healthy and are consuming enough food to maintain a positive energy balance.

The lack of food items in bull trout stomachs in this study support stable isotope results in that large bull trout are highly piscivorous (Chapman *et al.* 1989, Grey 2001), and likely feed in pulses (Boag 1987). Grey (2001) for example, found that large (>400 mm) piscivorous brown trout stomachs contained either fish, or were empty, as compared to smaller fish (300 mm range) that consistently had macroinvertebrates in their stomachs. Bull trout digest fish in about 12 hours (Armstrong and Blackett 1966); therefore the probability of sampling an adult bull trout with an empty stomach is relatively high. These results speak to the strength of S.I.A. which provides a temporally integrated description of what organisms eat.

Bull trout, unlike other sympatric salmonids, demonstrated continuous ontogenetic change in trophic profile – a potentially important life history character that would be lost if isotopic profiles were not assessed. Bull trout $\delta^{15}N$ values were positively correlated with length indicating that the fish occupy increasingly higher trophic positions as they grow in length. This ontogenetic shift was observed to a lesser degree in rainbow and cutthroat trout. Because bull trout attain a greater size than other salmonids in eastern slope systems, they can rely solely on piscivory, whereas rainbow and cutthroat trout are more omnivorous at full size as and eat less fish compared to bull trout (Scott and Crossman 1973, Boag 1987, Nelson and Paetz 1992). Mountain

whitefish and brook trout $\delta^{15}N$ values varied little with size and S.I.A. indicated that they rely almost exclusively on macroinvertebrates. As expected, the degree of ontogenetic shift (indicated by regression values) was directly related to the relative importance of other fish in the species' diet. It should be noted that large brook trout were rare in the Elbow River. If they were available, large brook trout samples would likely be similar to those of cutthroat and rainbow trout feeding primarily on invertebrates and occasionally on small fish (Scott and Crossman 1973, Nelson and Paetz 1992). Comparing inter-specific ontogenetic shifts using S.I.A. is unique to published works and comparable studies are not available. More research in this area is necessary to further illustrate salmonid food resource selection through time.

Reconstruction of the foodweb illustrated several interesting isotopic anomalies. Several individual whitefish and juvenile bull trout had $\delta^{15}N$ values higher than those of some adult bull trout. It is possible that whitefish signatures are inflated because they are feeding on ^{15}N enriched macroinvertebrates located downstream of the sampling area. Popowich and Williamson 2005 (unpublished. data) found a positive relationship between downstream distance from the Elbow River headwaters and $\delta^{15}N$ values in Dipterans, Ephemeropterans, and Plecopterans – all primary food sources of mountain whitefish (Scott and Crossman 1973, Nelson and Paetz 1992). With respect to inflated juvenile bull trout, it is possible that some individuals adopt piscivory at sizes smaller than the 300 mm size partition used in this study.

Also, $\delta^{13}C$ values in the food web reconstruction are considerably more enriched per trophic level than would be expected based on published standards (~ 1‰ relative the diet (DeNiro and Epstein 1978). This is especially true for baseline macroinvertebrates

that are 3 -5 ‰ enriched relative to the second trophic grouping of fish. While the 1‰ / trophic level standard has become commonplace since its first appearance in the literature (DeNiro and Epstein 1978), other studies since have shown that large (3 -5 ‰) $\delta^{13}C$ shifts per trophic level are not uncommon (Gu *et al.* 1996, Vander Zanden and Rasmussen 1999, Beaudoin *et al.* 2001), and are perhaps more widespread than generally appreciated. Additionally, isotope signatures in lotic invertebrates are variable and dependant upon individual variation, mobility, and spatial distribution (Lancaster and Waldron 2001). Doucett *et al.* 1996 argue allocthonous and autochthonous productivity are site specific, thereby contributing to $\delta^{13}C$ variability. Because baseline macroinvertebrate samples were collected from a small 6 km reach, these signatures may not be appropriate to compare against organisms that are free to move and feed throughout the entire watershed.

There are several limitations to the results of the isotopic reconstruction of the Elbow River foodweb including sampling breadth, acknowledgement of fish movement, and anthropogenic inputs. Samples should be collected from all representative size classes of all potential bull trout prey items. Noticeable exceptions here are terrestrial macroinvertebrates and vegetation known to be present in bull trout diets (Tripp *et al.* 1979, Boag 1987, Wilhelm *et al.* 1999). Juvenile mountain whitefish, brown trout, and members of non game fish genera such as Catostomidae, and Cottidae are also absent from this analysis. Although these fish were not present in the sampling area, these species do occur at lower reaches of the river (Fitzsimmons *et al.* 2002) and may be incorporated into bull trout diets during fluvial migrations.

Microhabitat and prey selection

Differentiating between the relative importance of prey distributions versus habitat type as factors influencing bull trout habitat selection is difficult, as they likely co-vary with abiotic habitat variables shown to be associated with bull trout occurrence (Watson and Hillman 1997, Paul and Post 2001, Rich *et al.* 2003,). These relationships are inter-related and their significance is dependant upon the spatial and temporal scales at which they are studied as well as dynamic attributes inherent to fluvial systems (Dunham and Rieman 1999, Hauer *et al.* 1999, Spangler and Scarnecchia 2001, Rodtka 2005).

The combination of abundant prey and low bull trout densities enables individual predatory bull trout to select optimal foraging habitat with lower levels of competition and predation. Bull trout in the Elbow River are clearly utilizing other fish as a primary source of energy, yet they are spatially segregated from their primary prey. High condition factors suggest that bull trout are not resource limited and S.I.A. coupled with stomach content analyses suggest a highly piscivorous diet. Therefore, bull trout in low densities, may adopt a sit-and-wait strategy and forage opportunistically since prey pursuit costs are unnecessary. Since food resources are not a factor limiting distribution, bull trout habitat selection behaviour appears to be driven by other variables, such as pool habitat.

If the density dependant hypothesis holds true, it is logical that stream macroinvertebrates and juvenile bull trout would comprise a greater proportion of adult bull trout diets (due to increasing intra-specific competition) at higher densities of bull

trout. Unfortunately, S.I.A. was not performed on the Sheep River. A density dependant prey selection study (using S.I.A.) would be an interesting addition to this work as it would likely reveal trends in prey use with respect to spatial associations between predator and prey at a variety of densities. With respect to habitat selection in populations with densities higher than the Sheep River, increased competition for pool habitat would likely drive greater numbers of subordinates to peripheral areas meaning that juvenile bull trout would be found at higher densities in run / riffle habitats. Higher predator to prey ratios would also force bull trout to invest greater amounts of energy towards prey pursuit and therefore, predator-prey spatial relationships would likely increase in strength before reaching a state of equilibrium.

Conclusion and implications for conservation

Observed patterns of habitat use are not static properties but rather depend on intrinsic factors such as population dynamics and density dependence as well as extrinsic factors such as abiotic habitat variables (Greenberg 1994, Mushens 2003, Shepherd and Litvak 2004). Habitat selection studies should take these factors into consideration prior to planning experiments. Habitat quality, including prey populations, has been shown to be critical to bull trout persistence and habitat disturbance is frequently listed as a major cause of decreasing population numbers. Focal species, food sources, and prey preferences should be given more attention as these resources may prove critical to continued population viability.

Here, it was demonstrated that bull trout habitat selection is a dynamic process. Through time, habitat requirements change. The question of how the relative importance of prey or pool habitat, for example, changes at different bull trout densities is an

important one. From a management perspective, the importance of determining critical habitat components is clear, however, it seems equally important to understand how the relative importance of these factors changes through time.

Table 1. Densities (fish/m^2) of bull trout in 6 km sections of the Elbow and Sheep Rivers. Densities were calculated using snorkel counts conducted throughout summer and fall 2004. Bull trout densities in the Sheep River were consistently higher throughout the sampling period. BLTR refers to bull trout of all sizes whereas adult bull trout refers to all bull trout > 300 mm FL.

River	Date (2004)	BLTR density (fish / m^2)	Adult BLTR density (fish / m^2)
Elbow	22-Jul	8.33E-05	2.27E-05
Elbow	31-Jul	3.64E-04	2.27E-04
Elbow	5-Aug	4.24E-04	2.35E-04
Elbow	15-Aug	4.55E-04	2.58E-04
Elbow	2-Sep	2.73E-04	1.74E-04
Elbow	19-Sep	1.59E-04	1.21E-05
Elbow	2-Oct	2.27E-05	2.27E-05
Sheep	20-Jul	4.05E-04	3.81E-04
Sheep	27-Jul	4.52E-04	4.29E-04
Sheep	1-Aug	1.11E-03	1.06E-03
Sheep	1-Sep	1.24E-03	1.24E-03
Sheep	18-Sep	9.88E-04	9.76E-04
Sheep	3-Oct	1.19E-04	1.19E-04

Table 2. Pearson correlation values describing the relationship between spatial distributions of predatory bull trout (>300 mm) and all potential prey species (brook trout, brown trout, cutthroat trout, mountain whitefish), including juvenile bull trout (<300 mm). No significant spatial relationships were found between predatory bull trout and their prey in the Elbow River at any point in time. In contrast, significant spatial relationships between predatory bull trout and their prey were found through July, August, and into September 2004.

River	Date	*r**	*p* value	α**
Elbow	22-Jul	-0.117	0.375	0.007
	31-Jul	0.030	0.822	0.007
	5-Aug	0.133	0.310	0.007
	15-Aug	0.167	0.203	0.007
	2-Sep	0.060	0.651	0.007
	19-Sep	0.140	0.188	0.007
	2-Oct	-0.009	0.944	0.007
Sheep	20-Jul	0.443	*<0.001*	0.008
	27-Jul	0.640	*<0.001*	0.008
	1-Aug	0.532	*<0.001*	0.008
	1-Sep	0.491	*<0.001*	0.008
	18-Sep	0.308	0.017	0.008
	3-Oct	0.113	0.391	0.008

Note: * *r* denotes Pearson's correlation coefficient, ** displays Bonferroni adjusted α values.

Table 3. Bull trout habitat selection during summer and fall 2004 on the Elbow and Sheep rivers described using chi-square scores. Observed values were established using fish counts collected during snorkel surveys. Expected values were calculated by multiplying snorkel counts by habitat (pool vs. run / riffle) estimates. Juvenile bull trout (<300 mm) in the Sheep River were rarely encountered and insufficient numbers were found to be included in the analyses (with the exception of the 1-Aug snorkel survey). Results indicate strong selection for pool habitat, especially in adults, with the exception of run / riffle selection in the Sheep River (Sept. 18) during spawning.

		Swim date (2004)	Sample size (n)	Chi square score	Significance	Comments
Juveniles	Elbow	22-Jul	9	9.8	p<0.01	pool selection
	Elbow	31-Jul	19	0.3	n.s	*
	Elbow	5-Aug	25	4.4	p<0.05	pool selection
	Elbow	15-Aug	26	0.1	n.s	*
	Elbow	2-Sep	13	3	n.s	*
	Elbow	19-Sep	5	0.6	n.s	*
	Sheep	1-Aug	4	0.7	n.s	*
Adults	Elbow	31-Jul	37	13.1	p<0.001	pool selection
	Elbow	5-Aug	31	10.3	p<0.001	pool selection
	Elbow	15-Aug	34	62.5	p<0.001	pool selection
	Elbow	2-Sep	23	42.9	p<0.001	pool selection
	Elbow	19-Sep	16	6.4	p<0.05	pool selection
	Elbow	2-Oct	3	10.7	p<0.01	pool selection
	Sheep	20-Jul	32	8.4	p<0.01	pool selection
	Sheep	27-Jul	37	22.8	p<0.001	pool selection
	Sheep	1-Aug	91	31.1	p<0.001	pool selection
	Sheep	1-Sep	100	106.8	p<0.001	pool selection
	Sheep	18-Sep	82	5	p<0.05	run / riffle selection
	Sheep	3-Oct	10	21.3	p<0.001	pool selection

Note: n.s., no significance

Table. 4. Mean number of fish observed in six randomly chosen 100 m survey sections on the Elbow River by 1 through 5 snorkelers. Counts for brook trout and brown trout were included in the mean number of fish observed however counts were not sufficient for species specific analyses. Significant differences were found between mean counts made by 1 through 5 snorkelers (repeated measures ANOVA $p = 0.03$).

Snorkelers	Mean number of fish observed (+/- SD)	Mean bull	Mean whitefish	Mean cutthroat
1	1.4 (+/- 3.4)	0.3 (+/- 0.8)	6.2 (+/- 6.5)	1.7 (+/- 1.4)
2	2.2 (+/- 4.6)	0.7 (+/- 0.5)	10.2 (+/- 6.9)	2.2 (+/- 2.0)
3	2.3 (+/- 4.7)	1.3 (+/- 1.4)	10.3 (+/- 7.1)	2.0 (+/- 1.8)
4	2.3 (+/- 4.1)	0.7 (+/- 0.6)	9.5 (+/- 5.6)	2.8 (+/- 1.9)
5	2.7 (+/- 4.6)	1.7 (+/- 1.4)	10.2 (+/- 7.5)	3.0 (+/- 2.0)

Note: SD, standard deviation

Table 5. Correlation coefficients calculated between bull trout and prey species at 8 randomly selected sites on the Elbow and Sheep Rivers. Correlation values vary through time and no consistent patterns are present indicating that sample sites can be treated as independent through time. Correlation coefficients are relatively low because individual site values are presented as relative proportions of all fish over 60 sample sites.

Survey R^2	1	2	3	4	5	6	7	8
Elbow	0.0051	0.0228	0.0233	0.0261	0.0261	0.0000	0.0104	0.0449
	0.0564	0.0418	0.0299	0.0229	0.0229	0.0000	0.0035	0.0449
	0.1077	0.0000	0.0000	0.0033	0.0033	0.0000	0.0035	0.0000
	0.0308	0.0380	0.0199	0.0327	0.0327	0.0873	0.0000	0.0337
	0.0205	0.0114	0.0100	0.0131	0.0131	0.0000	0.0000	0.0000
	0.0051	0.0000	0.0166	0.0033	0.0033	0.0079	0.0000	0.0000
Sheep	0.1371	0.1946	0.2191	0.2222	0.0588	0.0596	*	*
	0.0403	0.0268	0.0225	0.0000	0.0131	0.0000	*	*
	0.0323	0.0067	0.0281	0.0000	0.0196	0.0132	*	*
	0.0161	0.0067	0.0056	0.0444	0.0196	0.0000	*	*
	0.0000	0.0067	0.0169	0.0000	0.0065	0.0000	*	*
	0.0645	0.0000	0.0730	0.0000	0.0458	0.0728	*	*

Note: * no data

Table 6. Pearson correlation coefficients (r) describing variation between $\delta^{15}N$ and $\delta^{13}C$ signatures of repeated analyses of duplicate samples. All correlations were significant with the exception of $\delta^{15}N$ ratios of rainbow and cutthroat trout. Repeated samples for each of these species were highly correlated (> 0.95), however sample sizes ($n = 3$ for both species) were too low for the correlations to be statistically significant. Correlation values for all repeated measures of $\delta^{15}N$ and $\delta^{13}C$ suggesting that isotope preparation techniques, laboratory analyses, and subsequent results are reliable.

Group	Isotope	Sample size	*r*
All species*	δ15N	31	0.99
BLTR		12	0.99
MNWH		6	0.99
CTTR		3	0.95
RNTR		3	0.95
BKTR		7	0.99
All species*	δ13C	31	0.99
BLTR		12	0.99
MNWH		6	0.99
CTTR		3	0.99
RNTR		3	0.99
BKTR		7	0.98

*BLTR, MNWH, CTTR, RNTR, BKTR

Table 7. Mean species-specific differences between $\delta^{15}N$ and $\delta^{13}C$ signatures of anal vs. adipose fins for all species (rainbow trout included), bull trout (BLTR), mountain whitefish (MNWH), cutthroat trout (CTTR), and brook trout (BKTR). Statistical tests used are likely too powerful and differences are not likely biologically meaningful; duplicates within 0.5 ‰ are considered to be consistent. Taking this into consideration, significant biological differences were found between anal and adipose $\delta^{13}C$ signatures in all species (grouped), bull trout, and mountain whitefish and $\delta^{15}N$ signatures in brook trout. These results are inconsistent among species and between isotopes.

	$\delta^{15}N$ (mean +/- SD)	$\delta^{13}C$ (mean +/- SD)	*n*
All	0.28 +/- 0.23	0.74 +/- 0.50	83
BLTR	0.27 +/- 0.23	0.91 +/- 0.49	39
MNWH	0.26 +/- 0.18	0.90 +/- 0.42	20
CTTR	0.27 +/- 0.25	0.36 +/- 0.34	16
BKTR	0.55 +/- 0.22	0.10 +/- 0.08	6

Note: Rainbow trout were not included in individual species analyses due to small sample sizes.

Table 8. Species-specific variation between $\delta^{15}N$ and $\delta^{13}C$ signatures of anal vs. adipose fins (*p* values calculated using paired samples *t*-test). Significant differences were found between anal and adipose $\delta^{15}N$ signatures in all species (grouped), bull trout, and brook trout, and $\delta^{13}C$ signatures in bull trout, mountain whitefish, and cutthroat trout. These results are inconsistent among species and between isotopes.

Group	Isotope	Sample size	*p* value
All species*	$\delta^{15}N$	83	< 0.001
BLTR*		39	0.010
MNWH		20	0.070
CTTR		*16*	0.116
BKTR*		6	0.002
All species	$\delta^{13}C$	*83*	0.123
BLTR*		39	< 0.001
MNWH*		20	< 0.001
CTTR*		16	0.008
BKTR		*6*	0.196

Note: * indicates significant values

Figure 1. Map of the study area along the eastern slopes of the Rocky Mountains in Alberta, Canada, showing study areas (snorkel survey sections and the isotope sampling area (Elbow River only).

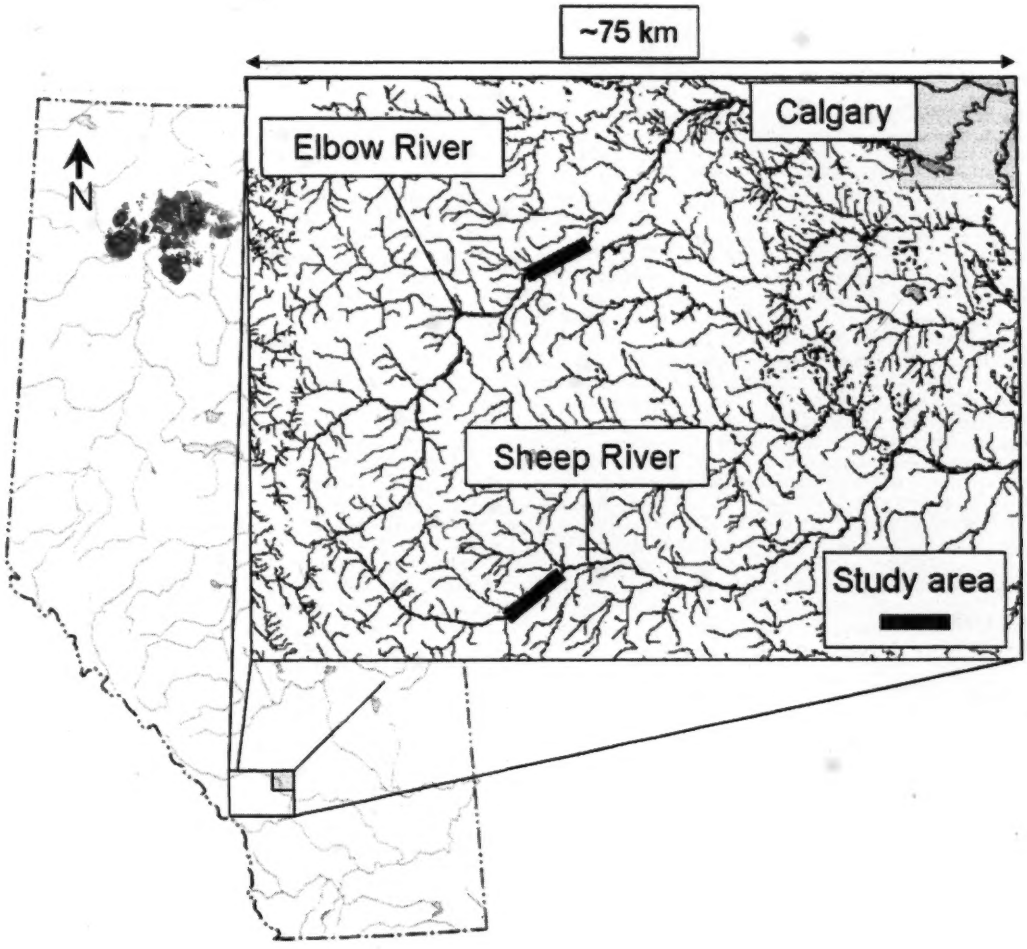
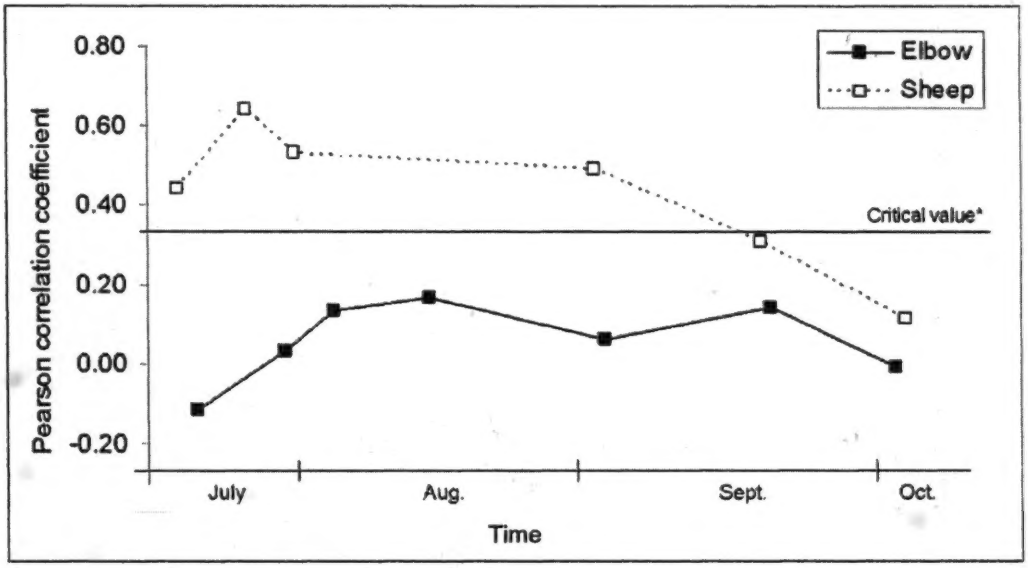


Figure 2. Pearson correlation coefficients describing the spatial relationship between bull trout and prey fish during summer and fall 2004 in the Elbow and Sheep rivers. Significant relationships were found on the Sheep river until late September when adult fish shifted energy focus from active foraging to spawning. Although no significant relationships were found in the Elbow River the pattern is similar to that in the Sheep River. Patterns in spatial relationships between bull trout and prey fish are similar to water temperature profiles for the rivers suggesting that increasing temperatures, and hence metabolism, result in increased foraging.



*Critical value (0.33) after Bonferroni correction

Figure 3. Discharge (m^3 / s) of the Elbow River. Data were collected at Bragg Creek, AB (Alberta Environment). Vertical bars indicate snorkeling date and associated values represent specific discharge values on snorkel survey dates.

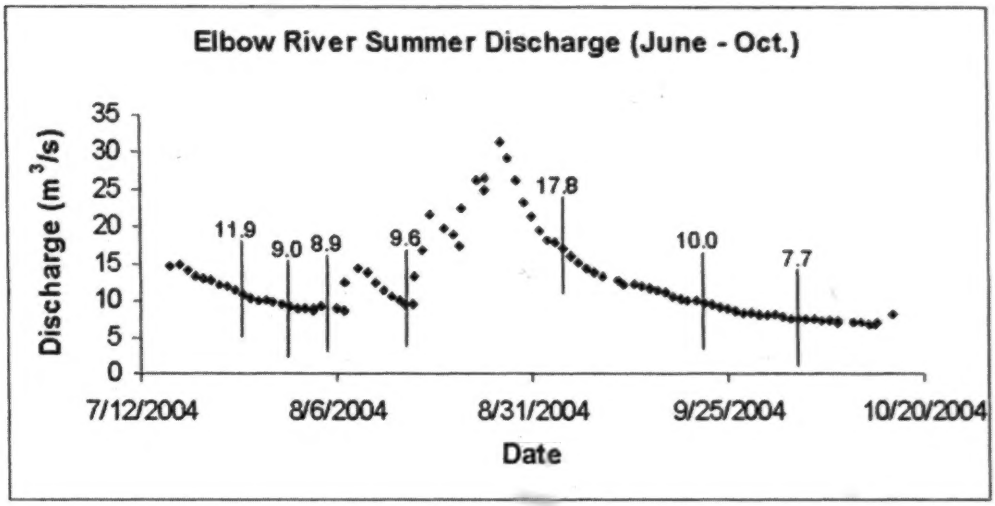


Figure 4. Discharge (m^3 / s) of the Sheep River collected at Black Diamond, AB (Alberta Environment). Vertical bars indicate snorkeling date and associated values represent specific discharge values on snorkel survey dates.

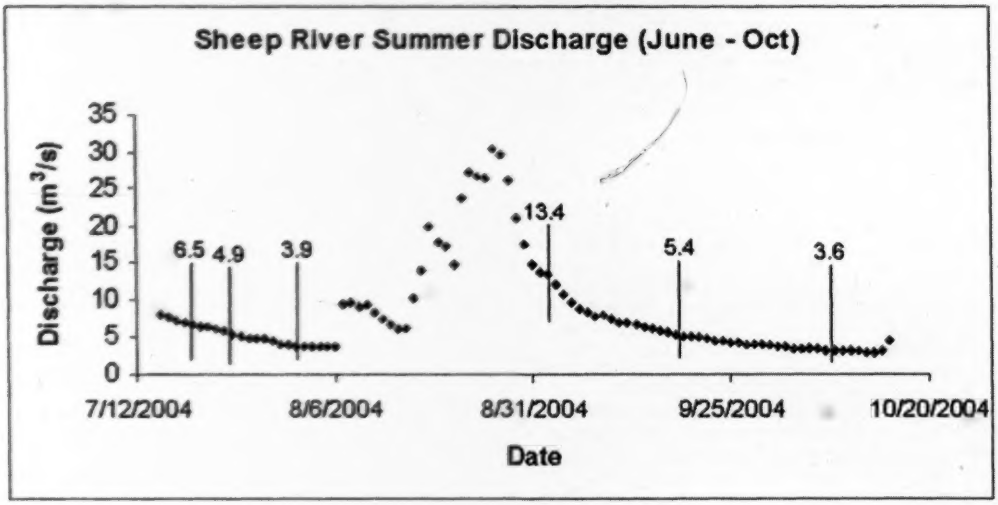


Figure 5. Summer temperature (°C) profile of the Elbow River in the snorkel survey reach. Vertical bars indicate snorkeling date and values represent mean daily temperatures.

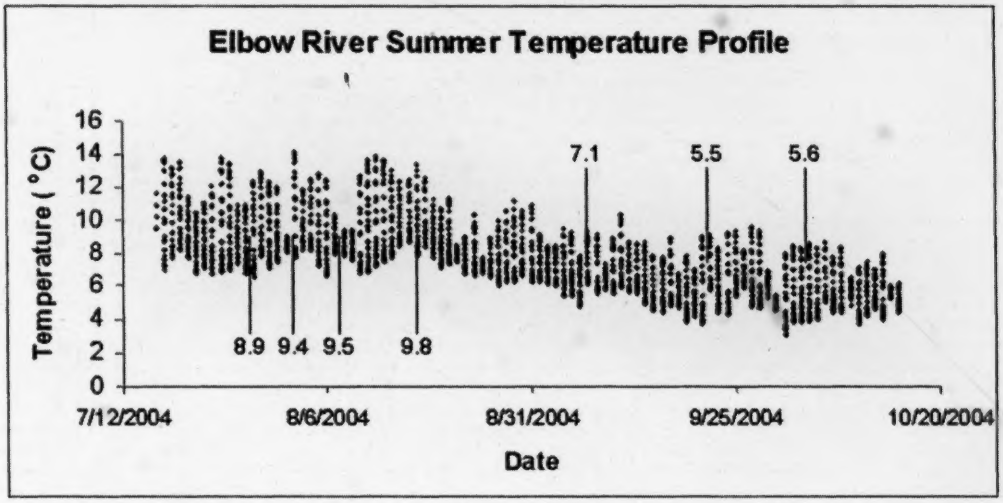


Figure 6. Relationship between $\delta^{15}N$ ratios established on duplicate runs of randomly chosen samples (all species).

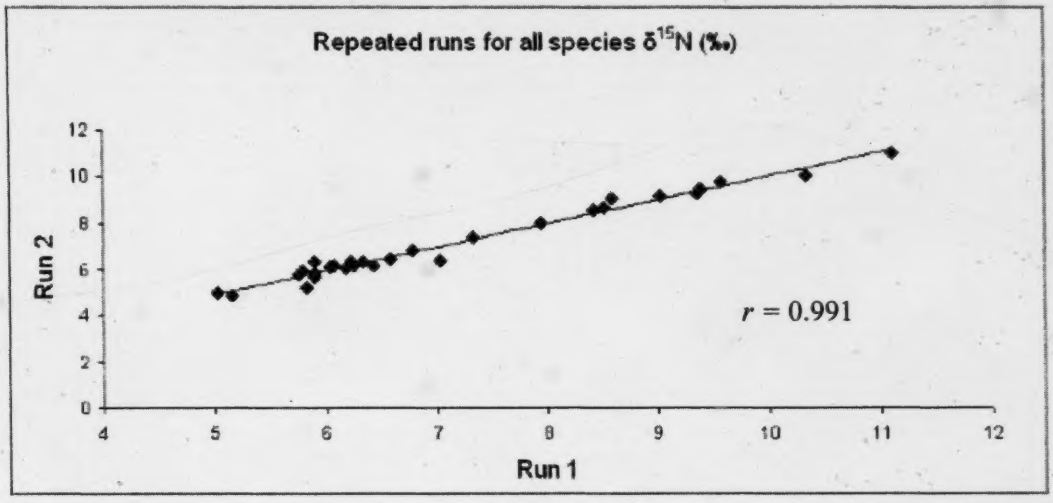


Figure 7. Relationship between $\delta^{13}C$ ratios established on duplicate runs of randomly chosen samples (all species).

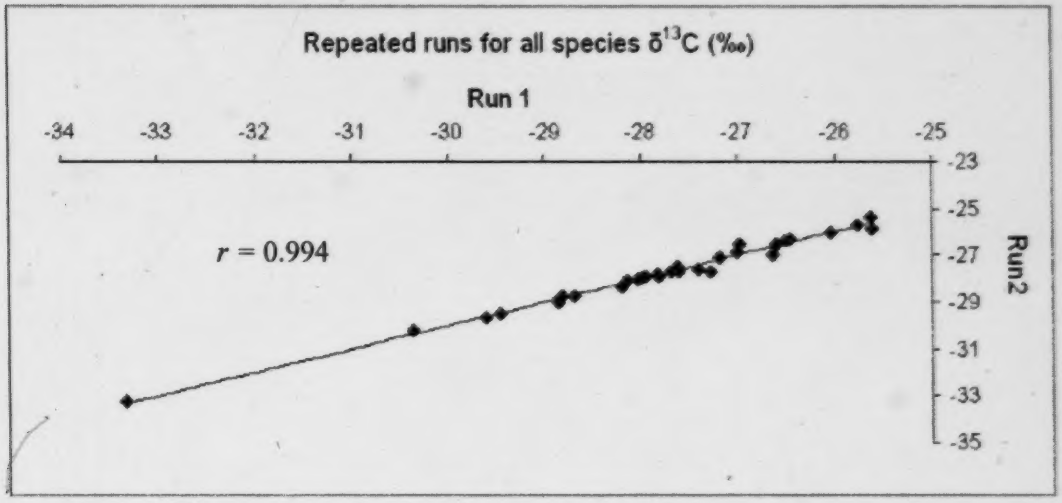


Figure 8. Relationship between $\delta^{15}N$ isotope ratios of anal and adipose fin tissue for all Elbow River fish species.

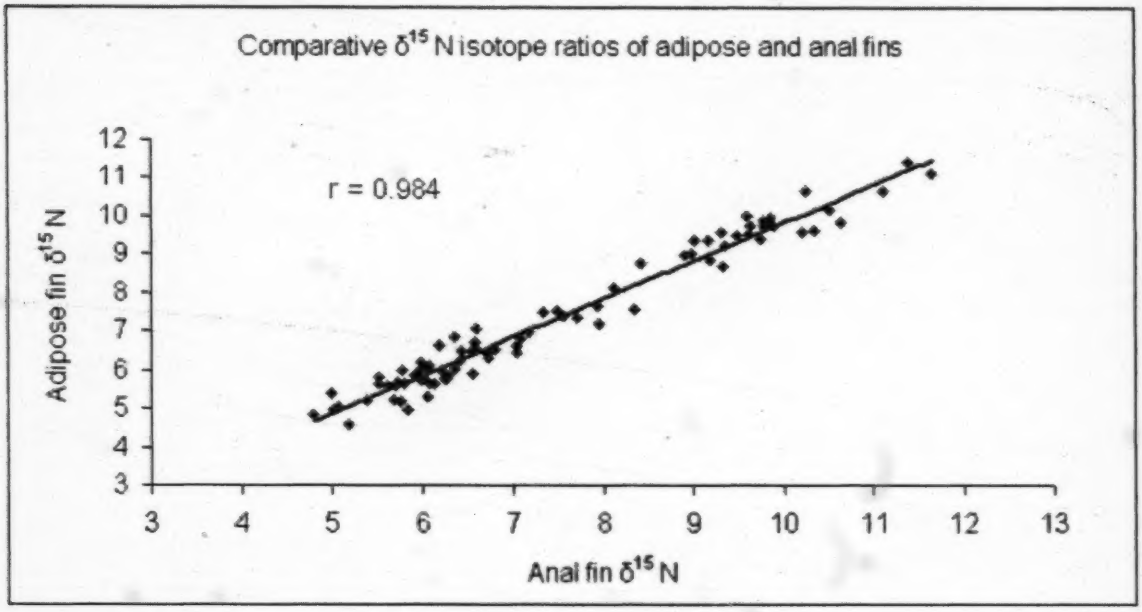


Figure 9. Relationship between $\delta^{13}C$ isotope ratios of anal and adipose fin tissue for all Elbow River fish species.

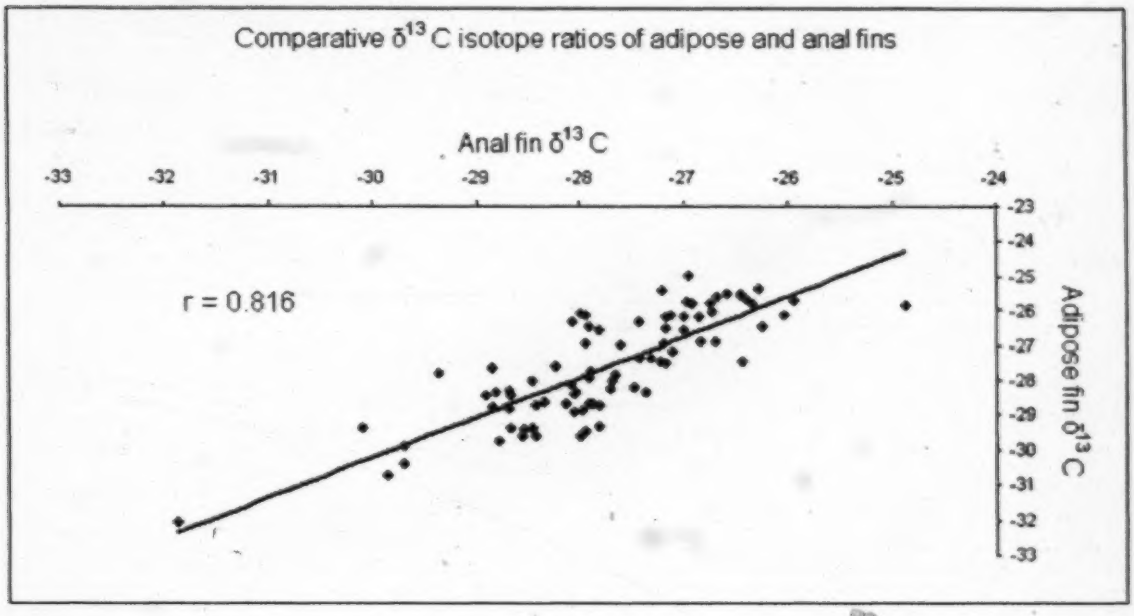


Figure 10. Tissue-dependant variability in mean $\delta^{15}N$ values for brook trout (1-way ANOVA). No significant differences were found between any of the tissues.

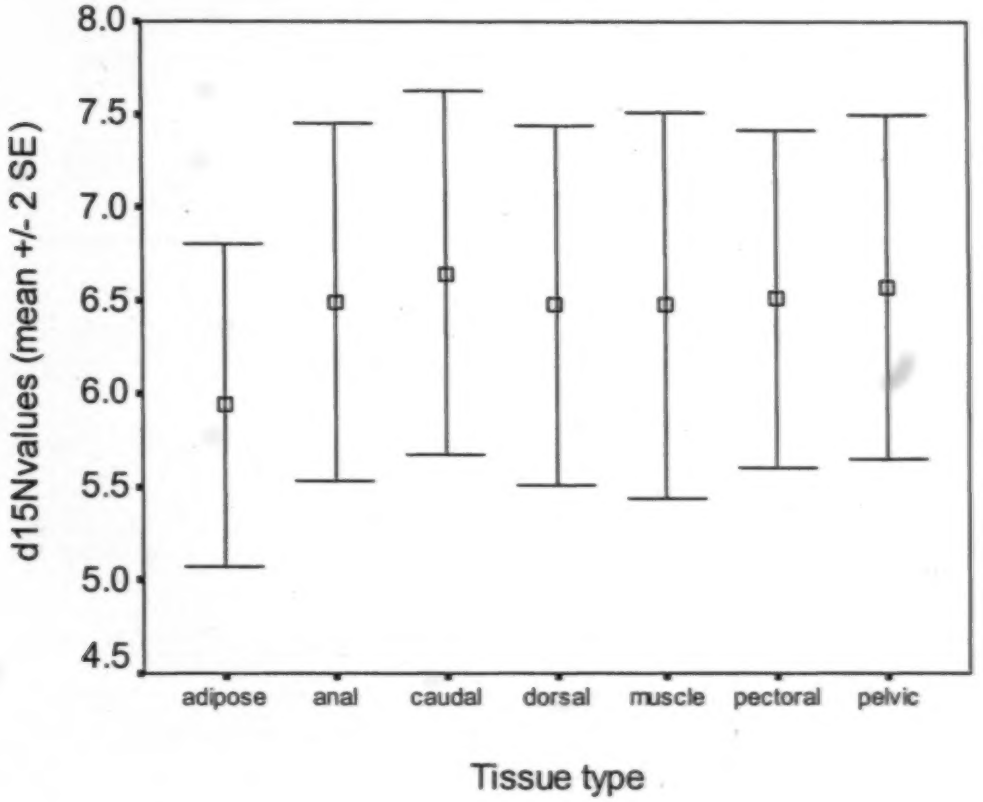


Figure 11. Tissue-dependant variability in mean $\delta^{13}C$ values for brook trout (1-way ANOVA). No significant differences were found between any of the tissues.

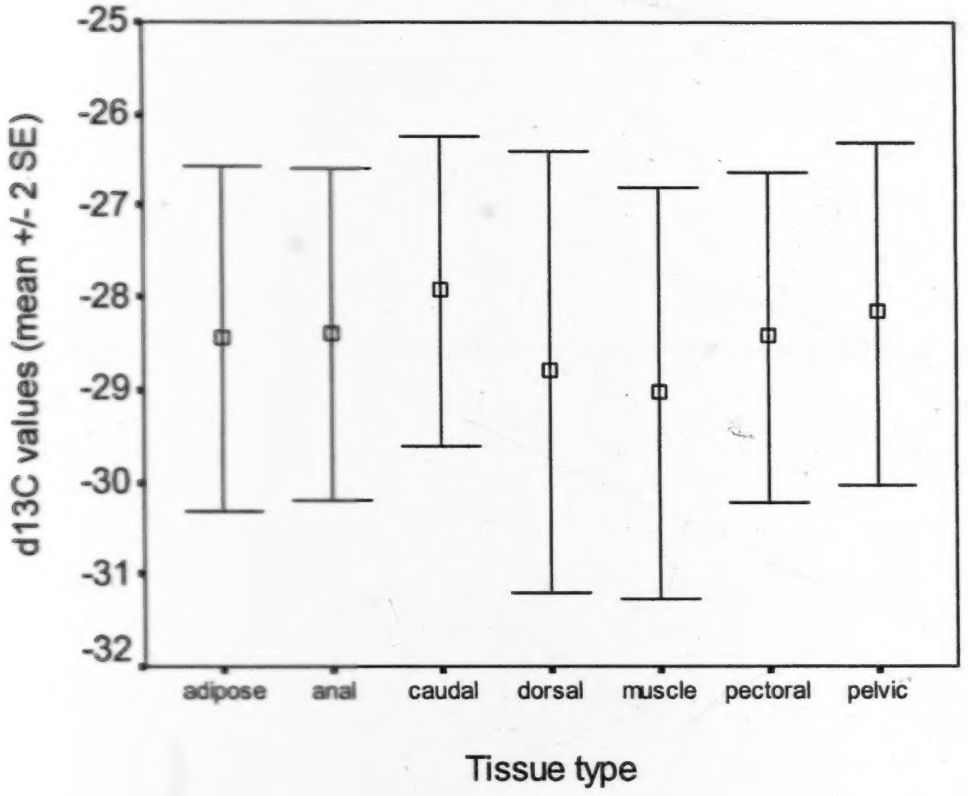


Figure 12. Reconstruction of the Elbow River food web using raw $\delta^{15}N$ and $\delta^{13}C$ values obtained from brook trout (bktr), bull trout (bltr), cutthroat trout (cttr), mountain whitefish (mnwh), rainbow trout (rbtr), and macroinvertebrates from the Orders Diptera (dipt.), Ephemeroptera (ephm.), and Plecoptera (plec.). Isotope signatures were obtained from anal fins for all fish species and whole organisms for aquatic macroinvertebrates. The food web reconstruction shows adult bull trout diets are comprised of brook trout, cutthroat trout, mountain whitefish, rainbow trout, and in turn, this fish grouping primarily preys upon stream macroinvertebrates.

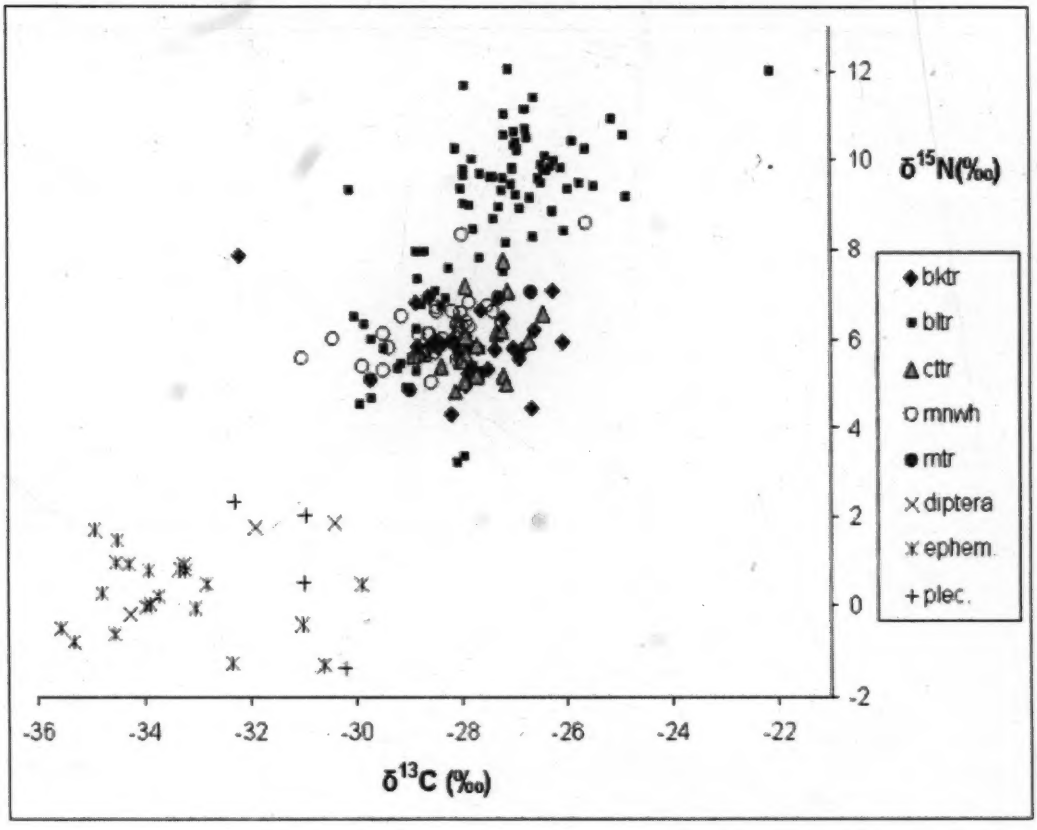


Figure 13. Reconstruction of the Elbow River foodweb using mean values (+/- SD) of $\delta^{15}N$ and $\delta^{13}C$ values from brook trout (bktr), bull trout (bltr), cutthroat trout (cttr), mountain whitefish (mnwh), rainbow trout (rbtr), and macroinvertebrates from the Orders Diptera, Ephemeroptera (ephem.), and Plecoptera (plec.). Isotope signatures were obtained from anal fins for all fish species and whole organisms for aquatic macroinvertebrates. The food web reconstruction shows adult bull trout diets are comprised of brook trout, juvenile bull trout, cutthroat trout, mountain whitefish, rainbow trout, and in turn, this fish grouping primarily preys upon stream macroinvertebrates. This figure clearly illustrates three distinct trophic groupings; i) primary consumers represented by stream macroinvertebrates, ii) secondary consumers comprised of brook trout, juvenile bull trout, cutthroat trout, rainbow trout, and mountain whitefish, and finally iii) adult bull trout as tertiary consumers.

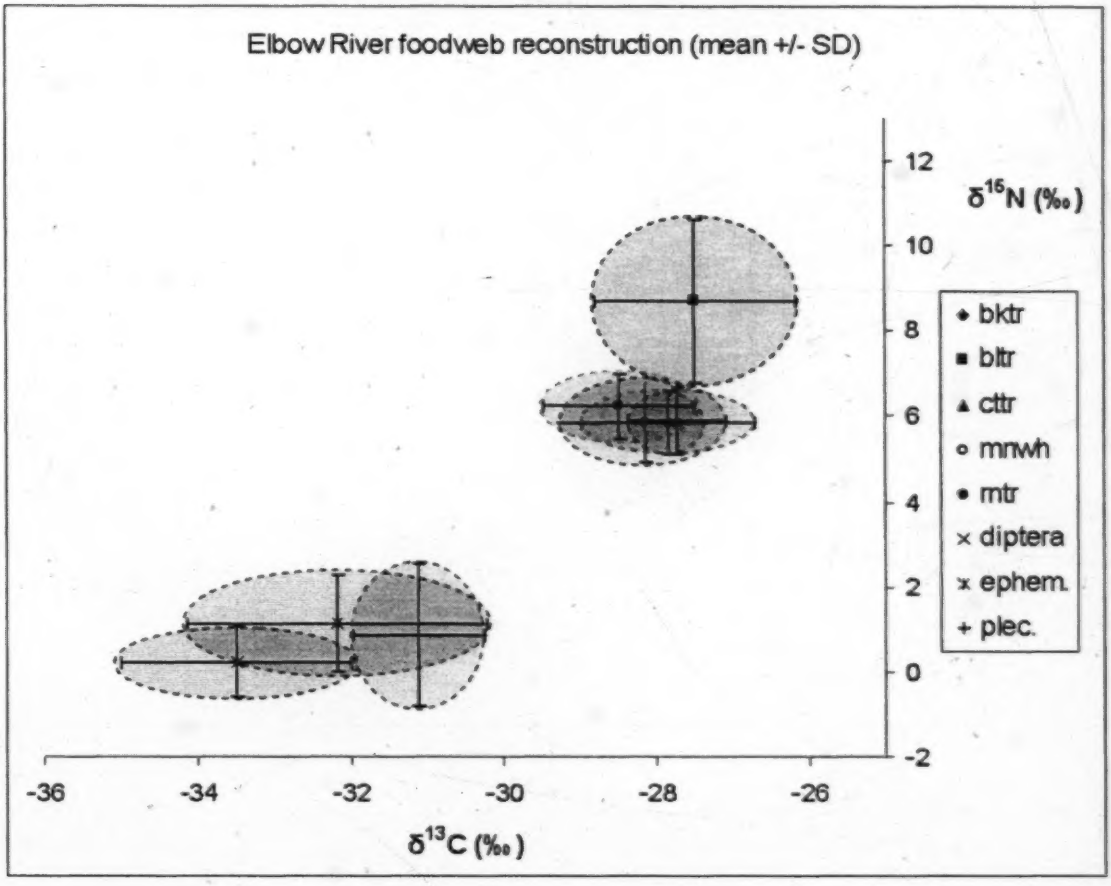


Figure 14. Reconstruction of the Elbow River foodweb using mean values (+/- SD) of $\delta^{15}N$ and $\delta^{13}C$ values of brook trout (bktr), juvenile bull trout (<300 mm) (juv. bltr), predatory (adult) bull trout (>300 mm) (pred. bltr), cutthroat trout (cttr), mountain whitefish (mnwh), rainbow trout (rbtr), and macroinvertebrates from the Orders Diptera (dipt.), Ephemeroptera (ephm.), and Plecoptera (plec.). Adult bull trout clearly occupy the top trophic position and prey upon brook trout, juvenile bull trout, cutthroat trout, mountain whitefish, and rainbow trout.

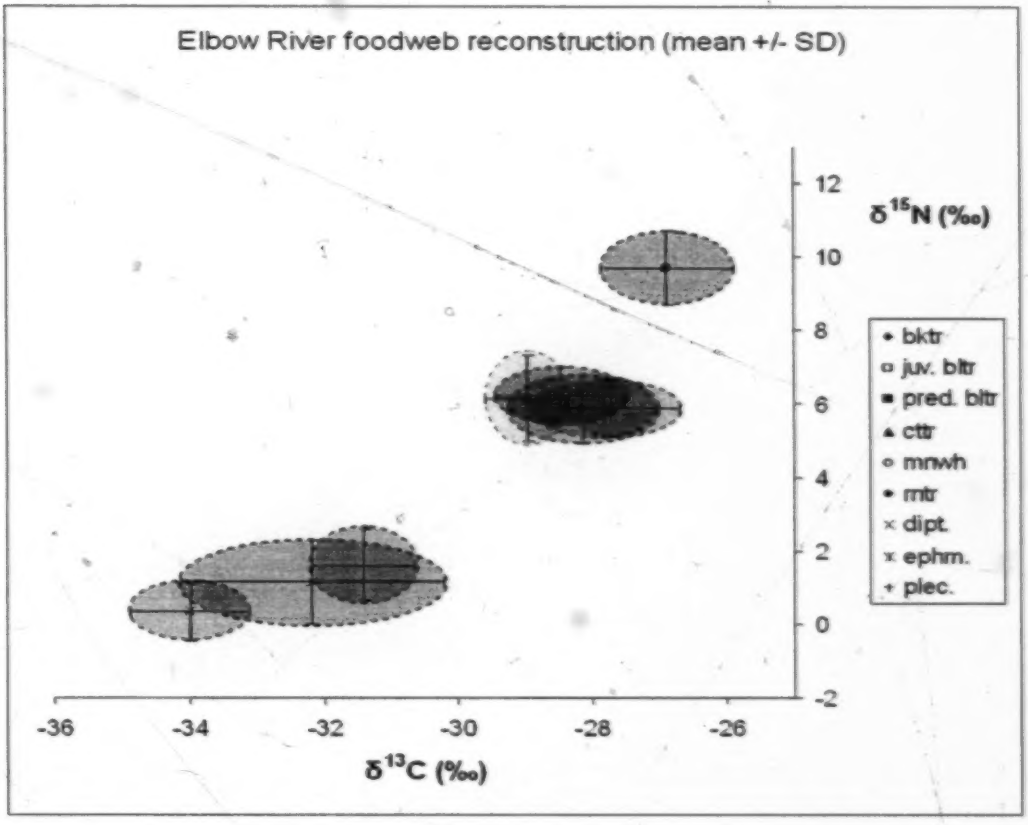


Figure 15. Relationship between fish length using raw $\delta^{15}N$ values for brook trout (bktr), bull trout (bltr), cutthroat trout (cttr), mountain whitefish (mnwh), and rainbow trout (rbtr). Bull trout $\delta^{15}N$ values were positively correlated with length indicating that the fish occupy increasingly higher trophic positions as they grow in length. This ontogenetic shift was observed to a lesser degree in rainbow and cutthroat trout. Mountain whitefish and brook trout $\delta^{15}N$ values varied little with size, and S.I.A. indicated that they rely almost exclusively on macroinvertebrates.

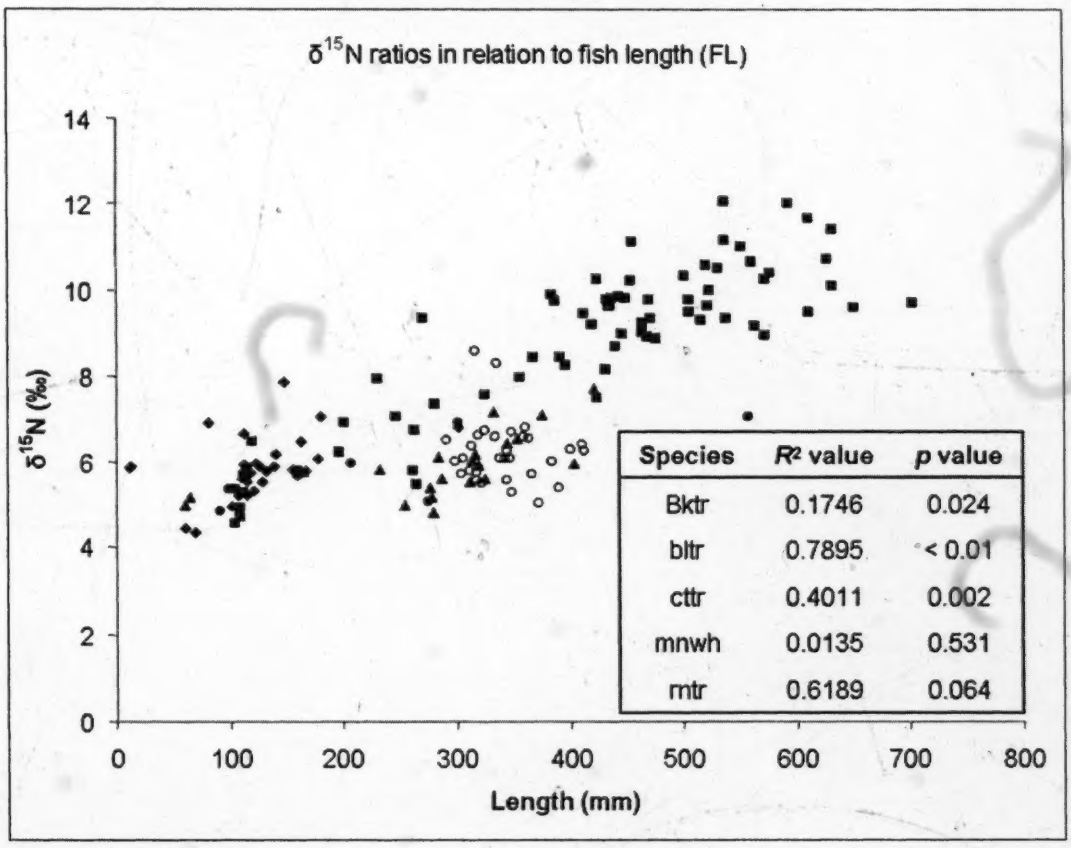


Figure 16. Evidence of dietary overlap in the Elbow River between native species (large bull trout excluded) (juvenile bull trout (<300 mm), cutthroat trout (cttr), mountain whitefish (mnwh)) and introduced species (brook trout (bktr), rainbow trout (rntr)) using mean values (+/- SD) of $\delta^{15}N$ and $\delta^{13}C$.

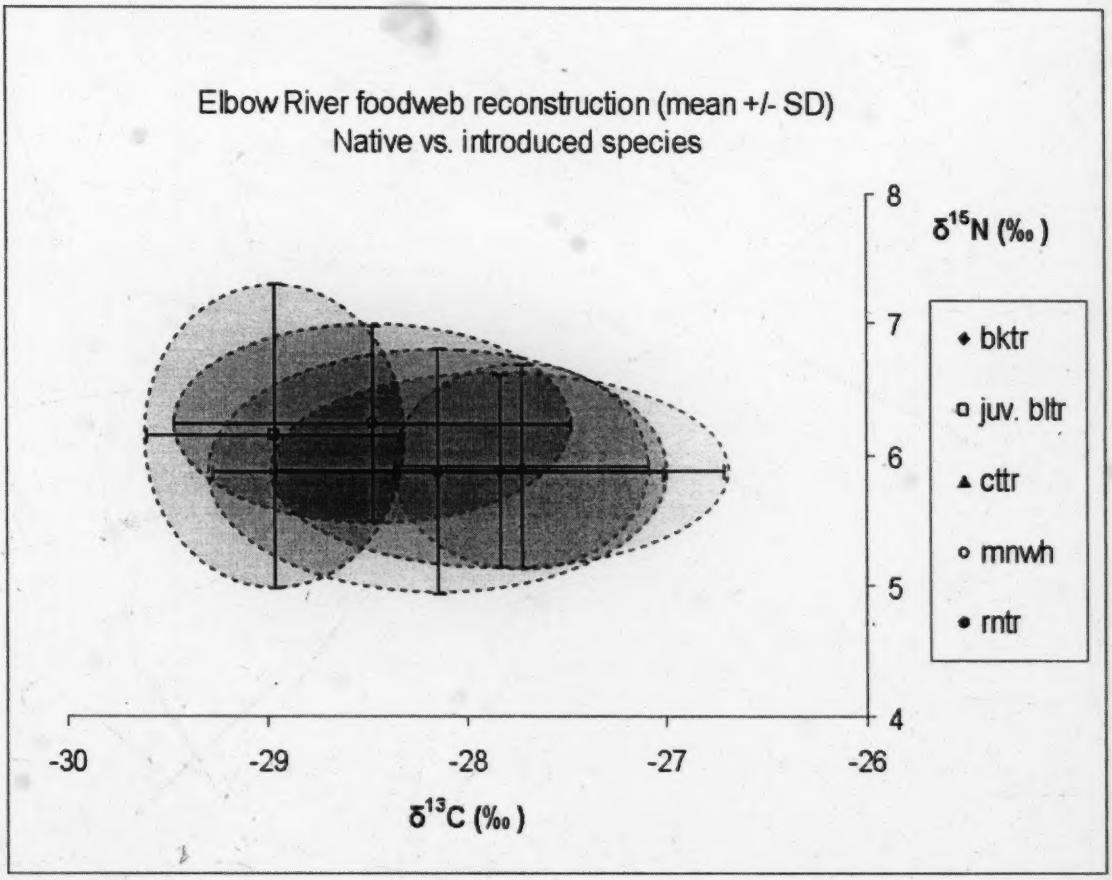
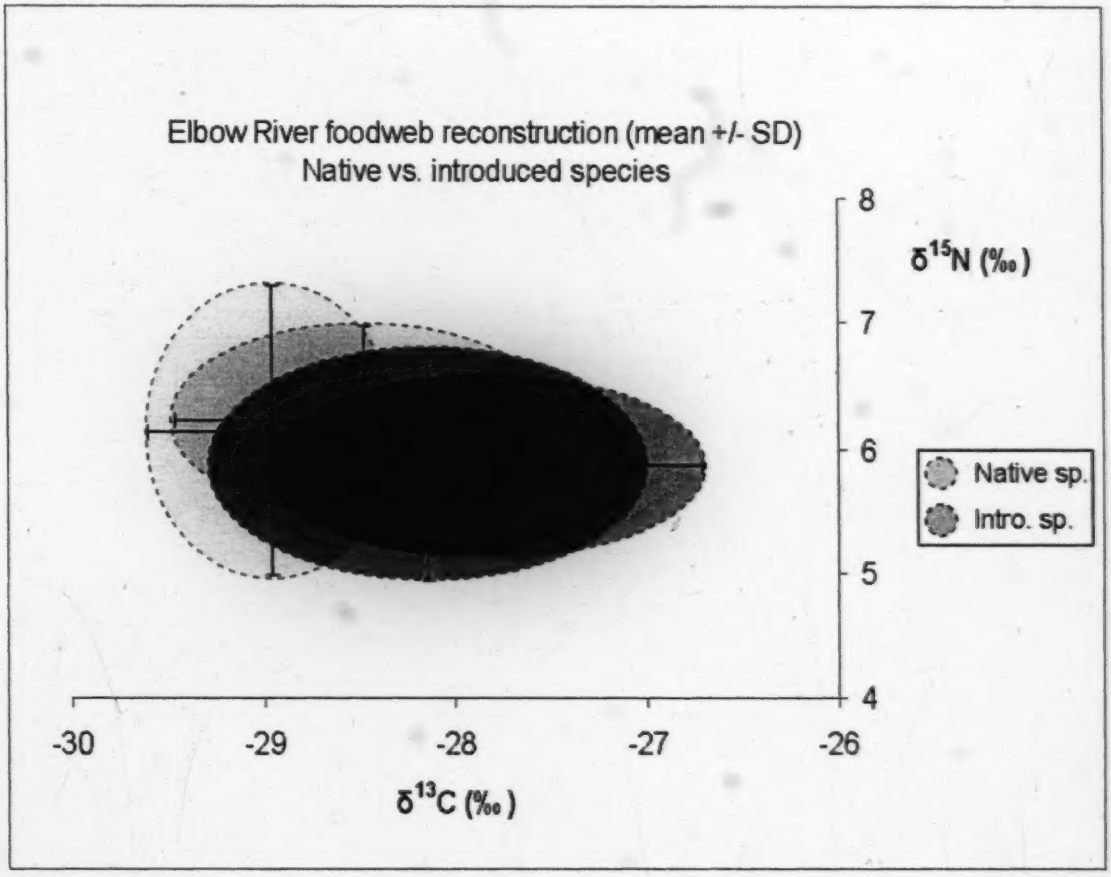


Figure 17. Graphic representation of competition in the Elbow River between native species (juvenile bull trout (<300 mm), cutthroat trout , and mountain whitefish) and introduced species (brook trout , rainbow trout) using mean values (+/- SD) of $\delta^{15}N$ and $\delta^{13}C$.



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